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IV. HOW MANY ARE THE KINGDOMS OF ORGANISMS? *

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Summary

The division of living organisms into Plantae and Animalia fails to recognise the major evolutionary discontinuity between prokaryotes and eukaryotes. In addition, fungi and "plant-animal" unicells lie uncomfortably in such a two-kingdom system. Systems have been proposed which separate prokaryotes from eukaryotes and divide the latter into several kingdoms. These schemes share two limitations. The "low" eukaryote kingdom (Protoctista or Protista) contains phyla more closely related to phyla of the "higher" kingdoms than to other phyla in the same kingdom. Secondly, the higher kingdoms are polyphyletic to a disturbing degree.

Can one make broad classifications without these limitations? A Prokaryota/Eukaryota two-kingdom scheme is one possibility; another is a four-kingdom scheme in which the protistan level is absorbed into the eukaryote kingdoms; a third possibility is a system in which phylum and phylogeny units stand as monophyletic kingdoms; such a multikingdom scheme provides fruitful scope for discussion. The Prokaryota/Eukaryota and multikingdom schemes allow flexibility for incorporation of new information on relationships, but may be thought too fragmentary for practical taxonomy. If so, various four- or five-kingdom schemes are available.

From the times of Aristotle and Galen, through the Middle Ages, through Bauhin's invention of the binomial system, through the floras and faunas of Linnaeus, Ray, Buffon and Réaumur, and up to modern times, biologists have described and named many hundreds of thousands of species of living organisms on the planet Earth. In attempts to present some order in this diversity, taxonomists and systematists have collaborated in arranging the species into groups, thereby producing various systems of classification. Earlier classifications, based at least partly upon superficial resemblances rather than evolutionary relationships, were artificial to a greater or lesser degree. The aim of modern systematics is that the classification shall be a "natural" one, reflecting true relationships as far as we can ascertain them from biochemical, cytological, morphological, developmental and behavioural features, from the fossil record, and from our understanding of heredity and evolution. Thus the more closely species are grouped in such a classification, the more closely related to one another they are thought to be. The system is *still* artificial, of course. Living organisms do not fit neatly into man-made categories; diversity is always continuous in some aspects.

Even so, as far as possible, closely related species are placed into the same genus, related genera into the same family, families into orders, orders into classes, classes into phyla or divisions, and phyla or divisions into kingdoms. It is the highest level in this hierarchy with which we are concerned here, and the problem in systematic terms is to decide what

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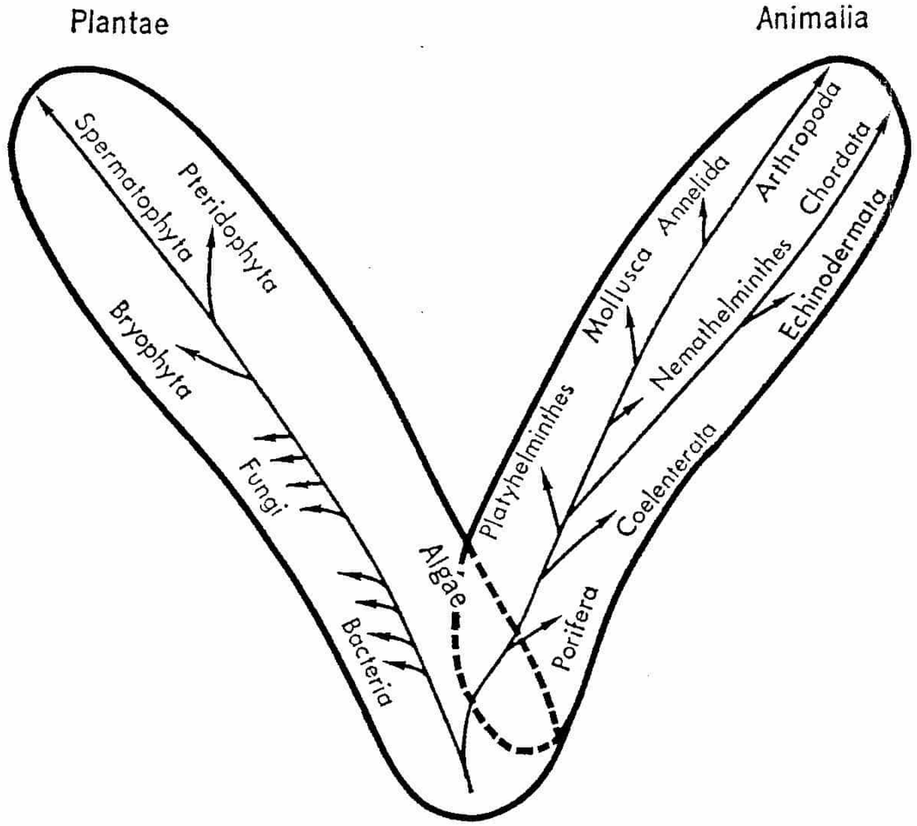

Fig. 1. Simple plant/animal two-kingdom evolutionary scheme; reproduced with kind permission from *Science* 163: 150-160. 1969 (fig. 1, R. H. Whittaker). Copyright 1969 by the American Association for the Advancement of Science.

broad evolutionary relationships we can discern among the phyla to allow grouping of these into our kingdoms.

The first kingdoms incorporated into the formal classifications of Linnaeus (1735) and others were those two groups of organisms that appeared obviously distinct to the early naturalists, the plants and animals. Such a two-kingdom system still seemed obvious two hundred years later at the beginning of the present century, the rooted habit and photosynthesis of plants being contrasted with the motility and food-ingestion of animals. Fungi, though non-photosynthetic, were thought of as rooted and could be placed with the plants; bacteria, though some are motile, have photosynthetic forms and could be grouped with plants by their possession of cell walls; food-ingesting, motile protozoa could be placed with the animals; and so on. Thus a Plantae/Animalia two-kingdom system (Fig. 1) was fully acceptable to most biologists.

The difficulties inherent in such a scheme have been summarised by Whittaker (1969) and others (the reader is referred to Whittaker's paper for an extensive list of contemporary and historical references and for detailed discussion of these).

Firstly, many unicellular organisms lie uncomfortably in the classical two-kingdom system, possessing combinations of characters that blur the distinction between plants and animals. The possibility of a third kingdom for lower organisms thus arises and was, in fact, proposed in various ways by Haeckel (1866) and others in the nineteenth century. Haeckel proposed

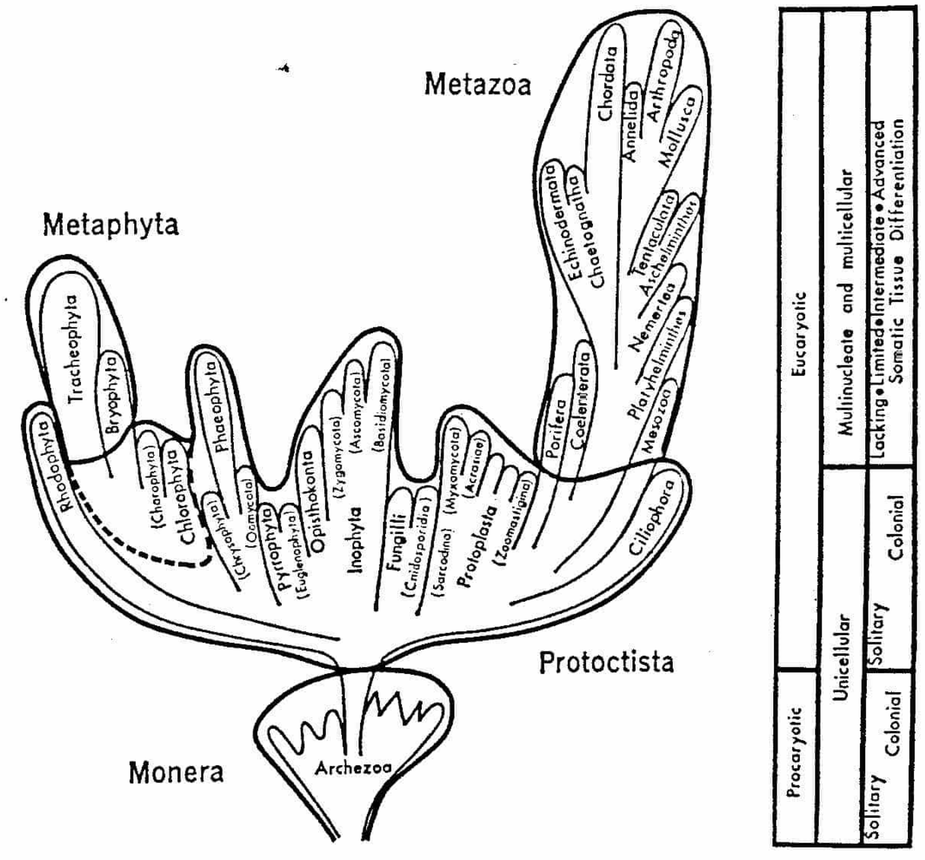

Fig. 2. Copeland's four-kingdom evolutionary scheme; as discussed by Whittaker, reproduced with kind permission from *Science* 163: 150-160. 1969 (fig. 2). Copyright 1969 by the American Association for the Advancement of Science.

the kingdom Protista for lower organisms lacking tissues and, in revised form (Haeckel, 1894, 1904), his kingdom came to contain only unicellular organisms (including bacteria which he placed in the subgroup Monera, protists without nuclei). Other schemes, including Haeckel's own earlier ones, grouped fungi, sponges and/or lower algae among the protists.

Secondly, in the classical two-kingdom system, bacteria and blue-green algae are included among the plants. Recent studies (see Stanier & van Niel, 1962; Margulis, 1970) have shown that the difference between prokaryotes and eukaryotes is more profound than any other separation of levels of organisation in living organisms. Prokaryotes (bacteria and blue-green algae) lack nuclei and chromosomes, lack other membrane-bounded organelles such as chloroplasts and mitochondria, and lack cytoplasmic structures such as 9+2 flagella, Golgi bodies and microtubules; prokaryote DNA is not combined with RNA and proteins; sexual systems are unidirectional. Eukaryotes (all other cellular organisms) have DNA complexed with RNA and proteins[1] in chromosomes within nuclei; their sexual systems involve gene exchange; complex organelles such as chloroplasts, mitochondria, 9+2 flagella and Golgi bodies are present. The two-kingdom system of classification fails to recognise this sharp demarcation.

[1] Excepting some dinoflagellates.

Thirdly, says Whittaker (1969), the fungi[2] differ fundamentally from true plants in their somatic organisation, reproductive systems, mode of nutrition, and so on. The two-kingdom system fails to recognise this difference.

From these points, Whittaker argues that the idea of two principal modes of nutrition in living organisms, plants primarily photosynthetic and animals ingestive, is now superseded by the idea of three main modes, photosynthetic, absorptive and ingestive, which largely correspond to the three ecological groupings of organisms as producers (the plants), reducers (bacteria and fungi) and consumers (the animals.) In each case the mode of nutrition has determined the evolution of the characteristics of the organisms and therefore forms a logical basis for a broad classification.

Such arguments underlie Whittaker's 1969 five-kingdom proposal (see below) and provide criticism of Copeland's earlier four-kingdom scheme (Copeland, 1938, 1947, 1956). In Copeland's system (Fig. 2) we have kingdoms separated on levels of organisation. Monera now stands as a separate kingdom for the prokaryotes; Protoctista comprises lower eukaryote unicells, colonies, syncitia and simple levels of multicellular organisation, i.e. algae, protozoa, slime moulds and fungi; Metaphyta consists of higher multicellular eukaryotes with green, walled cells, i.e. the "land" plants; and Metazoa comprises the multicellular animals.

The limitations of Copeland's system as criticised by Whittaker (1969) are, firstly, that one of Whittaker's three nutritional types, absorptive, is not demarcated; secondly, the Protoctista is such a wide assemblage of organisms that it appears more as a confederation of phyla excluded from the other kingdoms than as a kingdom in its own right; and, thirdly, it becomes impossible to draw a satisfactory boundary line between multicellular Protoctista and the higher plants and animals.

Whittaker therefore presented his 1969 five-kingdom system of classification (Fig. 3). In this the fungi form a separate kingdom and the line between protists and higher organisms is drawn at the transition from unicellular to multicellular. Hence we have the following five kingdoms: Monera for the prokaryotes; Protista for unicellular eukaryotes; Plantae for multicellular photosynthetic eukaryotes, the producers; Fungi for multicellular eukaryote reducers; and Animalia for multicellular eukaryote consumers.

Both Copeland's and Whittaker's schemes (and some with similar features by other authors, reviewed by Whittaker, 1969) are useful working concepts for contemporary biology, but they share two limitations. Firstly, Copeland's Protoctista and, to a lesser extent, Whittaker's Protista contain a heterogeneity of phyla. As indicated at the beginning of this paper, any grouping within a modern classification should aim to contain organisms that appear to be more closely related to one another than to organisms outside that grouping. This maxim should apply at the kingdom level just as much as at, say, the generic level. Yet the Protista of Whittaker, for example, contains phyla more closely allied to phyla of the three higher kingdoms than to other phyla in its own kingdom (Whittaker comments on this himself, of course). The Chrysophyta are a case in point, showing

[2] In detail, Whittaker's comments apply to the Zygomycete/Ascomycete/Basidiomycete line, though in his final 1969 scheme he also includes in Fungi the various groups of aquatic moulds that do not fit his generalisations so well.

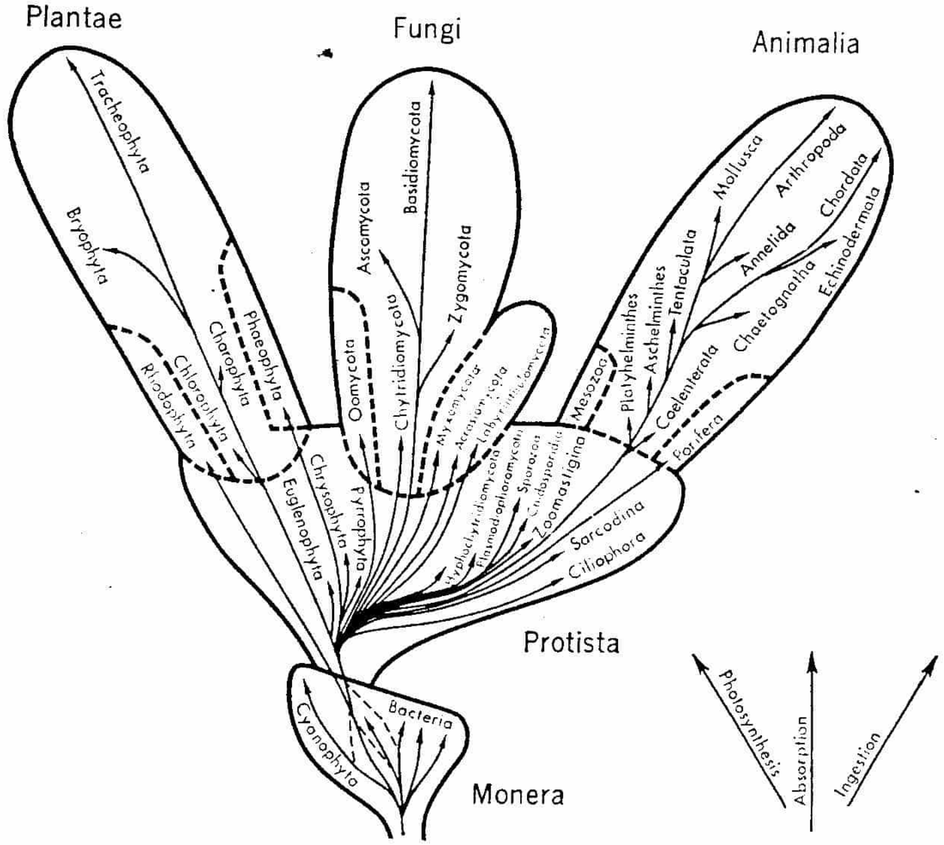

Fig. 3. Whittaker's five-kingdom evolutionary scheme; reproduced with kind permission from *Science* 163: 150-160. 1969 (fig. 3 R. H. Whittaker). Copyright 1969 by the American Association for the Advancement of Science.

strong affinities with Phaeophyta (Plantae) and Oomycota (Fungi) and no obvious affinities with Ciliophora or Sporozoa.

Secondly, higher kingdoms in both schemes are polyphyletic (on present ideas) to a degree that is profoundly disturbing to the ideal of a natural classification. Drawing the protistan line at the unicell/multicell boundary forces Whittaker to include Rhodophyta and Phaeophyta in Plantae with the green plants; Oomycota, Myxomycota, Acrasiomycota and Labyrinthulomycota with the "true" Fungi; and Mesozoa and Porifera with the Metazoa in Animalia. As Whittaker himself says, his three kingdoms of higher organisms appear less as kingdoms than as alliances of separate multicellular groups.

The main question for our discussion is, then, does a scheme like that of Copeland or Whittaker represent the best broad classification we can make at present, despite its acknowledged limitations, or are there sensible (better) alternatives?

Margulis (1971) has recently suggested a modification of Whittaker's system (Fig. 4). This removes phyla from Plantae, Fungi and Animalia into the upper reaches of the Protista, leaving the three kingdoms of higher organisms arguably monophyletic. It does, of course, increase the heterogeneity of the Protista and objections to that kingdom on those grounds. It is, in effect, a partial return to Copeland's scheme with the main exception of

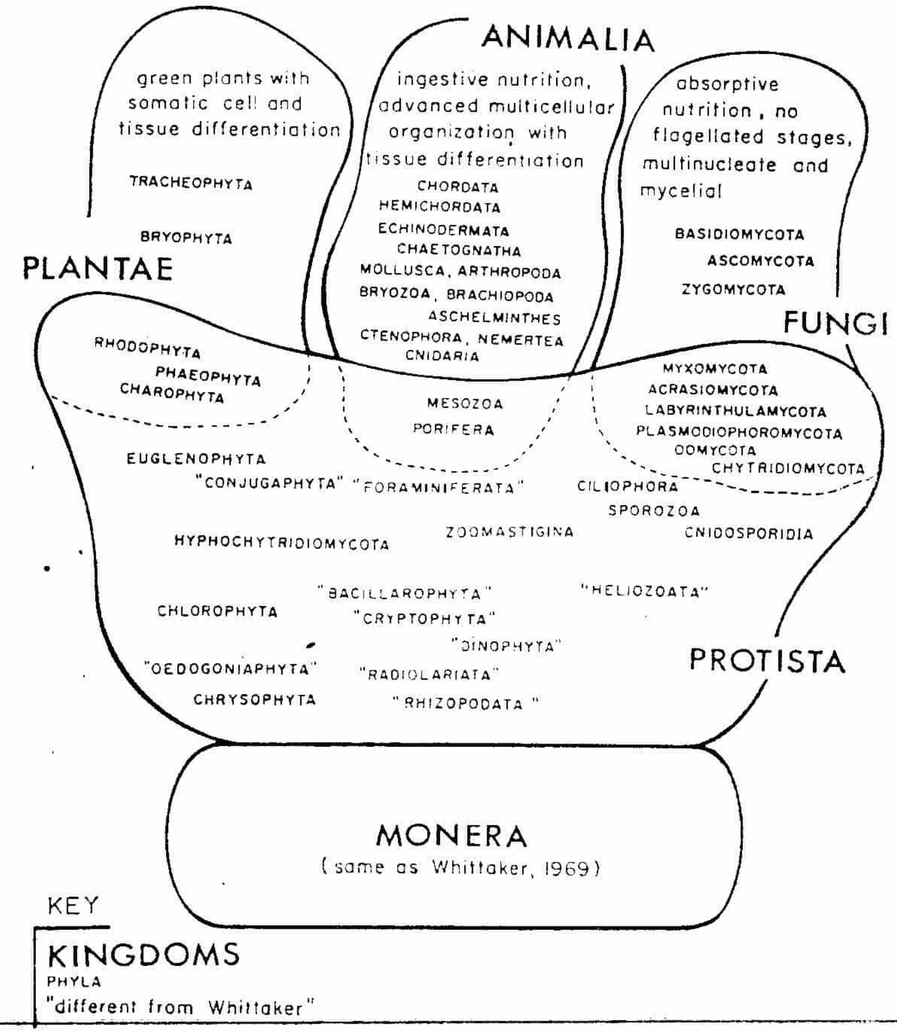

Fig. 4. Margulis' modification of Whittaker's five-kingdom evolutionary scheme; reproduced with kind permission from Evolution 25: 242-245. 1971 (fig. 2, L. Margulis). See Margulis (1974, refence this issue p. 226) for a detailed and up-to-date modification of Whittaker's five kingdom classification.

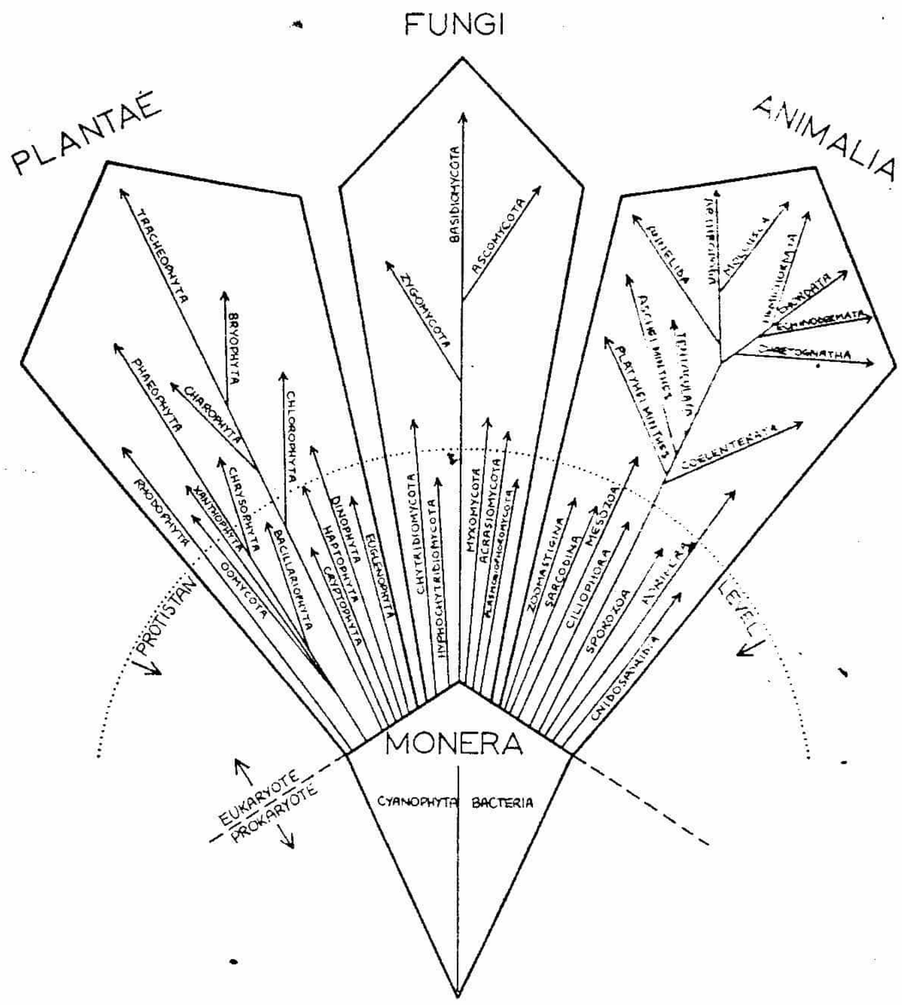

Fig. 5. "Pteropod" scheme: proposal for a four-kingdom evolutionary scheme in which the protists do not appear as a kingdom.

retaining Whittaker's absorptive nutrition group, now just the "higher" fungi, as a kingdom. Margulis' modification and comments on the Whittaker system are made, of course, in relation to evolutionary concepts of the serial symbiosis theory of origin of the eukaryotic cell (see Margulis, 1970), the broad principles of which are concerned with the transition from prokaryote to eukaryote by incorporation, into an anaerobic protoamoeboid, of a protomitochondrial symbiont, a protoflagellar symbiont, and, for the plant lines, a protoplastidial symbiont.

The sharp discontinuity between present-day prokaryotes and eukaryotes, and between these levels in the fossil record, can be accounted for either by the serial symbiotic process of "instant evolution" or by evolution of organelles by membrane deployment within the prokaryote/eukaryote intermediates (steps which we than have to presume are as yet undiscovered in present-day organisms and fossils, or are not represented because lost through evolution and non-preservation). It is important to note that the four- or five-kingdom Copeland/Whittaker/Margulis classifications are, in fact, consistent with *either* of these theories, whereas the classical plant/animal two-kingdom system is not.

Margulis (1974) argues that this latest modification does not suffer from the limitations Whittaker saw in his own 1969 system. However, it brings back to Whittaker's system two of the limitations he found in the scheme of Copeland and attempted to eradicate: firstly, the great heterogeneity of the "confederation" of protists, and, secondly, the impossibility of drawing a satisfactory boundary between multicellular protists and the higher plants and animals. So, again, the question arises, is this the best broad classification that can be devised at present or are there sensible alternatives? In particular, can we aim for organisms within kingdoms to be more closely related to one another than to organisms in other kingdoms?

It is surely agreed that the greatest discontinuity in living forms lies between prokaryotes and eukaryotes and this must appear in a modern

classification as a boundary between kingdoms (even though possession of a common genetic code, use of ATP in energy production, and so on, indicate that all life had common ancestry). So perhaps we should have a new two-kingdom system of Prokaryota and Eukaryota, with the Eukaryota containing numerous phyla which do not have to be grouped into kingdoms. The Copeland/Whittaker/Margulis problem of arranging the eukaryotes into three or four kingdoms is not solved but avoided.

Another alternative is a four-kingdom system in which the protists are dispersed and absorbed in the higher kingdoms (Fig. 5). A "protistan level" can be indicated in each of the three eukaryote kingdoms, but problem phyla such as Chlorophyta which have both "protistan" and "plant" members are accommodated. Furthermore, cases can be made on various grounds to suggest that organisms within each kingdom are more closely related to one another than to organisms in different kingdoms; or, at least, it is more difficult than in the Whittaker or Whittaker/Margulis schemes to pick phyla which *clearly* have close affinities with phyla in other kingdoms[3].

However, in this "pteropod" scheme, the degree of polyphyly in the eukaryote kingdoms is now even greater. Though it would be possible, on somewhat controversial grounds, to construct more theoretical phylogenies to interrelate the phyla than I have done here, we would still find problem phyla left on their own. If we try to resolve this by making every kingdom monophyletic (on present knowledge and ideas) we inevitably produce a multikingdom system of some sort (Fig. 6). In fact, this "fan" scheme is intended as a basis for argument rather than as a completed system. Thus only a selection of protozoan and animal phyla is shown and the "kingdoms" have not been given proper names. It is, however, instructive to note some features of the system.

Firstly, some "kingdoms" contain just one phylum, this in turn just one class, and this, in one case, the eustigmatophytes (see below), only the seven species known at present, perhaps carrying the idea of isolated taxonomic groups with peculiar features rather far for some tastes. Strictly, however, there is no logical objection to a kingdom containing *just one species*. If a species is so uniquely distinct in biochemical, cytological and morphological characters that it stands well apart from other taxa, it should be left in splendid isolation. There is no minimal group-size requirement for any taxonomic level. A really unique species may represent the sole present-day survivor of a large class, or phylum, or even kingdom. Its individuality should not be obscured by tucking it into another group for sake of neatness.

Secondly, each kingdom now arguably contains organisms more closely related to one another than to organisms in other kingdoms, and each is arguably monophyletic. Further, possible relationships among kingdoms can be indicated by their relative placings (though this soon becomes difficult). Thus, euglenoids show possible remote affinities with chytrids and Fungi *sensu stricto* (e.g. by possession of the α-amino adipic acid pathway for lysine synthesis) and also with zoomastigines (possible relationships to

[3] Exceptions might be the "lower" groups of fungi: some zoologists would certainly approve the removal of myxomycetes and ascrasiomycetes from Fungi into Animalia near to the Sarcodina. Also, one might try to take some account of possible affinities between euglenoids and certain zoo-flagellates (see below).

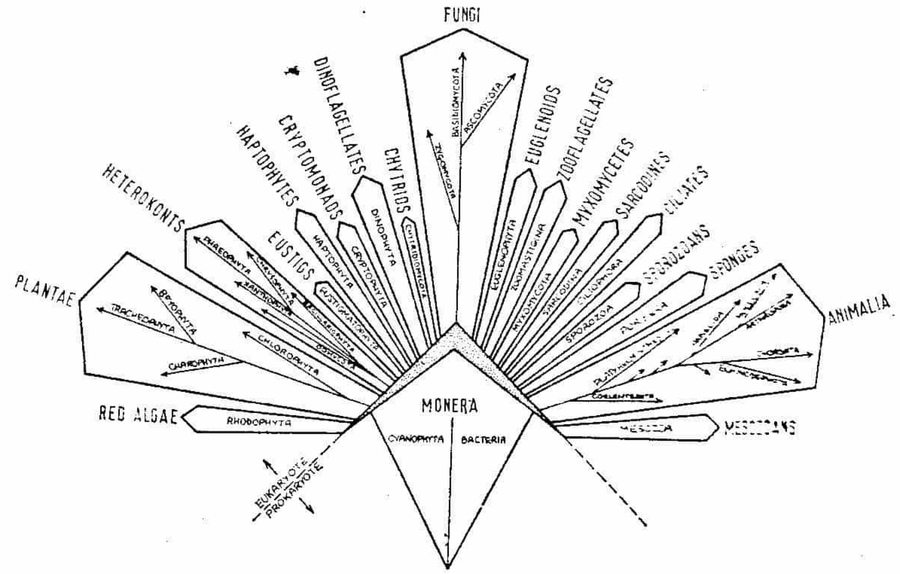

Fig. 6. "Fan" scheme: proposal for a multi-kingdom evolutionary scheme. The stippled area represents the missing link of present-day forms and of the fossil record: the period of cell symbiosis or organelle development.

trypanosomes on the basis of cytological features such as flagellar insertion and mitosis ultrastructure, now strongly supported by close cytochrome C affinity between *Euglena* and *Crithidia*). Plantae (including the green algae, Chlorophyta) is placed near the red algae and the heterokonts (e.g. by possession of cellulose in the cell wall) and further from chytrids and Fungi (most, at least, without cellulose; most with chitin in the cell wall). On the other hand, cytochrome c data should perhaps persuade us to push the Plantae and Animalia segments of the fan towards Fungi in the centre.

The phylogenetic grouping of the heterokonts is an important innovation in the scheme, placing organisms with heterokont flagellation *sensu stricto* (which implies numerous other features in common, see Massalski & Leedale, 1969; Hibberd & Leedale, 1971) into one kingdom (containing Phaeophyta, Chrysophyta, Xanthophyta, Bacillariophyta and Oomycota), Eustimatophyta (species originally in the Xanthophyceae but with fundamentally different organisation, see Hibberd & Leedale, 1972) and Haptophyta (originally in the Chrysophyceae, but ditto, see Christensen, 1962) appear as separate mini-kingdoms, as do other phyla that show more uniqueness than features in common. It might also be pointed out that problems such as the "classical" placing of euglenoids with green algae, and haptophytes with chrysophytes, on virtually the sole basis of the same or similar photosynthetic pigments, are ignored here, and can be nicely dealt with by invoking that part of the cell symbiosis theory which dates back to the last century, suggesting that quite separate evolutionary lines happened to acquire the same protoplastidial symbiont!

To summarise, at the broadest level of classification of phyla into kingdoms we are faced with the problems of how to deal with the prokaryote/eukaryote demarcation, how to deal with the diversity of unicellular eukaryotes, and how to deal with the valuable systematic principle of monophyly. We have seen that the classical plant/animal two-kingdom system fails to cope satisfactorily with these problems and that various better alternatives can be suggested.

In the light of recent studies, the sharp discontinuity between prokaryotes and eukaryotes seems to be the one boundary that is obligatory in a modern classification. However, in a two-kingdom system of Prokaryota and Eukaryota, the large number of phyla in the latter kingdom may be considered a practical disadvantage (though division of eukaryotes into a number of phyla and, possibly, groups of phyla (phylogenies) which are not formally named as kingdoms would allow flexibility for re-arrangement as new information sheds new light on relationships; the phylum and phylogeny units in such a two-kingdom system could be the same at present as those in the multi-kingdom scheme (Fig. 6.)).

If the Prokaryota/Eukaryota and multi-kingdom schemes are both considered too fragmentary for practical purposes, a four- or five-kingdom system is available as an alternative. As is implied in my four-kingdom scheme (Fig. 5), I find the term "protistan level" useful. The term can be clearly defined in relation to the non-cellular (i.e. unicellular, colonial and syncitial) level of organisation and one can sensibly discuss phyla which contain organisms at both the protistan and multicellular levels. As soon as one uses the term "Protista" (with a capital P) problems of definition and, especially, demarcation become acute. For this reason I find the proposed four-kingdom scheme (Fig. 5) preferable to the schemes of Copeland, Whittaker or Whittaker/Margulis (Figs 2-4). All four schemes clearly separate prokaryotes and eukaryotes but compromise our aim at a "natural" classification by containing obviously polyphyletic groupings, an objection not to be found (at least so blatantly) in the Prokaryota/Eukaryota two-kingdom scheme or in the related multi-kingdom system.

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